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A NEW SUBSPECIES OF *HULSEA VESTITA* (ASTERACEAE)

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The *Hulsea vestita* complex of California and Nevada comprises five currently recognized subspecies of self-incompatible, densely lanate, caespitose, herbaceous perennials with a dimorphic, quadripartite, paleoaceous pappus and a uniform diploid complement of 38 chromosomes (Wilken, 1975). Of particular interest within this complex is the occurrence in the western Transverse Ranges of southern California of populations that have been variously treated in several floristic works. Specific epithets applied to these populations include *H. callicarpa* (Hall) Rydberg, *H. parryi* A. Gray, and *H. vestita* A. Gray (Rydberg, 1914; Jepson, 1951; Keck, 1959; Ferris, 1960; Munz, 1974). Recently, I postulated (Wilken, 1975) that these populations represent an intergrading complex involving ssp. *vestita* and ssp. *parryi*. This hypothesis was based on observations of leaf morphology and ray flower number. Further study has revealed, however, that populations from the western Transverse Ranges, particularly the San Gabriel Mountains, display discordant variation with respect to presently circumscribed taxa. It is the purpose of this paper to discuss the relationships and status of these problematical populations by a numerical analysis of morphological variation and studies of synthetic hybrids.

MATERIALS AND METHODS

Field studies were begun in 1970 and seeds were collected to serve as a source of parental strains for an extensive crossing program. Methods with respect to crossing attempts and studies of meiosis and hybrid fertility (= pollen stainability and seed set) were as described elsewhere (Wilken, 1975). During the spring and summer of 1972, a series of populations, derived from 18 natural populations, were grown from seed to flowering maturity in a common garden at Occidental College, Los Angeles, California. These garden populations represented all recognized subspecies of *Hulsea vestita* and six populations from widely sepa-

rated sites in the San Gabriel Mts. (Table 1). Each of the garden populations comprised 10–18 plants and represented progenies of at least five randomly selected plants in each of the natural populations. Twenty vegetative and floral characters were chosen for measurement (Table 2). These characters have been shown to be the most useful in delimiting taxa within the complex (Wilken, 1973). The data were standardized by range and an unweighted analysis was performed, using Gower's Correlation Coefficient (Sneath and Sokal, 1973) and a program written for the CDC 6400 computer. Each of the 18 garden populations was treated as an OTU in the numerical analysis. A phenogram was constructed by using single-linkage clustering. Although variation of leaf shape and blade margin was valuable in assessing relationships, quantification of these characters for the numerical analysis was not done. Variation of leaves among garden populations is illustrated in Figure 1. Additional morphological studies were made of natural population samples, synthetic hybrids, and specimens borrowed from several herbaria (CAS, GH, JEPS, MO, NY, POM, RM, RSA, UC, UTC, WTU). Common garden and greenhouse populations were assigned the number corresponding to vouchers of natural population samples.

RESULTS

A phenogram of relationships (Fig. 2) reveals the distinctiveness of San Gabriel Mt. populations and supports the delimitation of accepted infraspecific taxa of the *Hulsea vestita* complex. The lowest level of similarity between OTUs representing a recognized taxon is 0.889 for ssp. *inyoensis*, whereas the highest level is 0.945 between OTUs and 8200

TABLE 1. LOCATIONS OF NATURAL POPULATIONS USED AS SEED SOURCES FOR THE CROSSING PROGRAM AND GARDEN POPULATIONS. Plants of all 18 populations were examined for chromosome number, which was uniformly $2n = 38$. All collections, with the exception of ssp. *inyoensis*, are those of the author (cited *W*). The two collections of ssp. *inyoensis* were provided by J. Beatley. Vouchers are deposited at CS.

California, Inyo Co., Cottonwood Meadows at head of Cottonwood Creek, *W* 4255. Los Angeles Co., Devil's Backbone, S slope of Mt. San Antonio, *W* 11891; E slope of Mt. Williamson, *W* 11890; 3 mi E of Chilao, *W* 11880; upper Tujung Canyon, 1.5 mi W of Highway 2, *W* 11879; along road to Mt. Pacifico, 2 mi E of Mill Creek Summit, *W* 11878; near summit of Mt. Gleason, 5 mi W of Mill Creek Summit, *W* 7946. Madera Co., near Rainbow Falls, Devil's Postpile N. M., *W* 8202. Mono Co., along Highway 120, 6.9 mi E of Highway 295, *W* 8200. Riverside Co., road to Toro Pk., 5.9 mi S of Highway 74, Santa Rosa Mts., *W* 7896; County Road R1, 8.6 mi NW of Idyllwild, San Jacinto Mts., *W* 7844; County Road R1, 1 mi S of Idyllwild, San Jacinto Mts., *W* 7858. San Bernardino Co., summit of Mt. San Gorgonio, *W* 8703; ridge between Fish Creek and Big Meadows, San Bernardino Mts., *W* 8703; Coon Creek, 3 mi SE of Highway 38, San Bernardino Mts., *W* 3047; along Highway 38, 2 mi E of Heart Bar Park, San Bernardino Mts., *W* 3048.

Nevada, Nye Co., SW face of Rainier Mesa, Belted Range, *Beatley* 9376; top of Rainier Mesa, *Beatley* 8836.

TABLE 2. CHARACTERS USED IN THE NUMERICAL ANALYSIS. Actual values were measured, recorded, and coded. Leaf and pubescence data were taken from the tenth leaf of the basal rosette. Pubescence density was determined by counting the trichomes within a 1 cm² square placed over the midrib at the center of the blade. Bract data were taken from the lowermost bract of the inflorescence. All capitulum and floral data were taken from the first mature capitulum.

Plant height (cm); Leaf length (mm); Leaf width (mm); Bract length (mm); Bract width (mm); Abaxial nonglandular pubescence density (number of trichomes per cm²); Peduncle length (cm); Number capitula per plant; Number of phyllaries per capitulum; Phyllary length (mm); Phyllary width (mm); Number of ray flowers; Ray corolla length (mm); Number disc flowers; Disc corolla length (mm); Achene length (mm); Narrow pappus pair length (mm); Broad pappus pair length (mm); Achene pubescence length (mm).

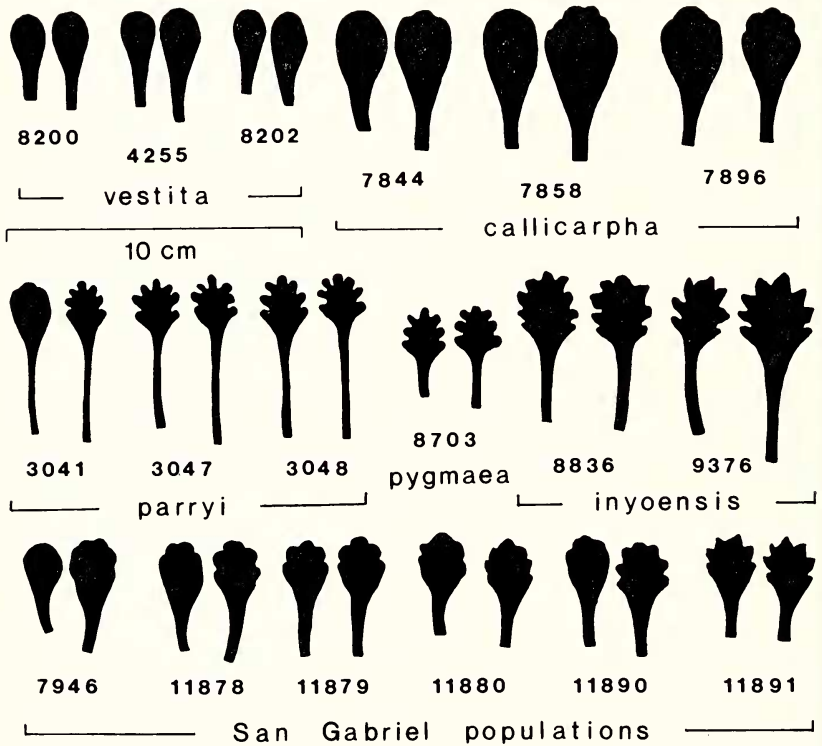


FIG. 1. Basal leaf silhouettes depicting range in size. Silhouettes were drawn from the tenth leaf of the basal rosette of common garden plants. Each pair represents the largest and smallest tenth leaf observed within each of the garden populations. Each number refers to the voucher of the natural population (= seed source).

and 8202 of *ssp. vestita*. The lowest level of similarity between the six problematical OTUs is 0.906, which is the overall similarity between OTU 11891 and the other five OTUs.

Phenetic relationships of the six San Gabriel OTUs indicate an alliance with *ssp. callicarpha*. Variation in garden populations of both groups overlapped with respect to a number of characters, including plant height, peduncle length, achene length, pappus length, and the number of phyllaries, ray flowers, and disc flowers. Basal leaf shape and size in San Gabriel populations are intermediate to those of *ssp. vestita* and *ssp. parryi*, but blade margin approximates that of *ssp. parryi* or *ssp. inyoensis*. There is a tendency toward subentire leaves in western populations in the San Gabriel Mt. (7936, 11878) and crenate to slightly

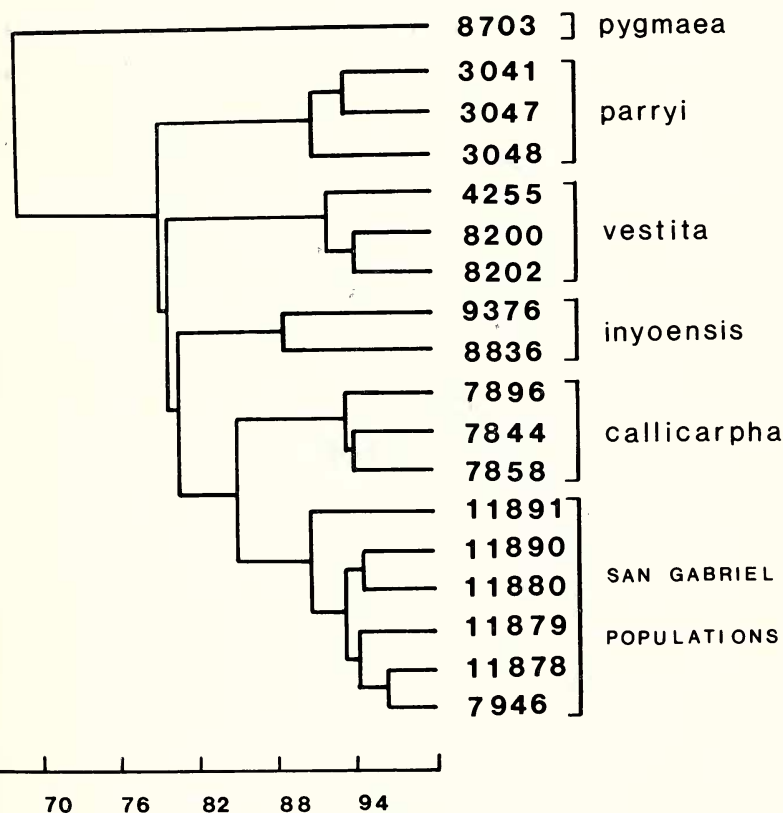


FIG. 2. Cluster diagram of 18 populations representing all infraspecific taxa within *Hulsea vestita* A. Gray. The phenogram was constructed using single-linkage clustering. The horizontal axis represents the correlation coefficient used in this study. Each number refers to the voucher of the natural population (= seed source).

subspecific) were not statistically significant. Germination ranged from 3 to 100% (ave. = 37), but no significant correlations with kinds of combinations were observed. Hybrids of all 18 intrapopulation and 91 interpopulation combinations were grown to flowering maturity and examined for meiosis and pollen stainability (Fig. 3). Nearly all hybrids, regardless of combination, were vigorous under garden and greenhouse cultivation. Normal meiosis and high pollen stainabilities characterized most hybrids. The lowest pollen stainabilities were in F_1 hybrids involving ssp. *pygmaea* as one parent. Observations of meiosis in these hybrids revealed the presence of either 17 bivalents and a chain of 4 chromosomes or 17 bivalents, a chain of 3, and 1 univalent. Most interspecific F_1 hybrids resembled the maternal parent with respect to peduncle length and plant height but were intermediate to both parental strains with respect to most other morphological characters.

DISCUSSION

Contrary to my earlier assessment that western Transverse Range populations represent an intergrading complex involving ssp. *vestita* and ssp. *parryi* (Wilken, 1975), the numerical analysis and review of morphological variation indicate that these populations possess a combination of characters unique within *Hulsea vestita*. These characters include subentire to crenate, spatulate leaves with relatively broad petioles, reddish-tinged, lanceolate to broadly obovate phyllaries, reddish-tinged corollas, and peduncles from 11–47 cm long. Most plants of natural populations may be distinguished by these characters. Furthermore, the use of data based on common garden plants suggests the genetic similarity of these populations. This distinctive morphology, combined with an allopatric distribution, leads to the conclusion that these populations represent a discrete taxon. Accordingly, I propose the following name:

***Hulsea vestita* ssp. *gabrielensis* Wilken, ssp. nov.**

Herbae perennes scaposae, 17–38 cm altae. Folia basalia spatulata, ca. 3–6 cm longa, ca. 1.0–2.5 cm lata, utrinque glandulosa et laxe lanata, margine integra vel crenulata vel rare crenata. Capitula plerumque numerosa, vel in plantis minoribus tantum 1–3, pedunculis 11–47 cm longis. Involucrum subcylindricum usque hemisphericum, ca. 2 cm latum, ca. 1 cm altum, phyllariis 3–4-seriatis, interiores oblongis vel anguste lanceolatis, exteriores lanceolatis vel late obovatis ex rubreo viridis. Flores radii 16–23, ex rubreo pallide flava. Flores disci 41–91, corolla ca. 6 mm longa, tubo gracili, lobis ex rubreo flavis, parce glanduloso, faucibus late cylindricis. Achaenia compresso-quadrangulata, ca. 5 mm longa, supra 1 mm lata, nigra, strigosa. Pappus ex 4 paleis, subequalis. Chromosomatum numerus: $n = 19$.

TYPE: California, Los Angeles Co., Angeles Crest Highway, 3 mi E of Chilao, San Gabriel Mts., 6000 ft., 1 Jun 1973, *D. H. Wilken 11880* (Holotype: RSA!; isotype: CS!, others to be distributed).

Distribution: Known from open, gravelly or disturbed sites within or marginal to the coniferous forest of the western Transverse Ranges of southern California from Frazier Mt., Ventura Co., east to Mt. San Antonio, Los Angeles Co.

Representative specimens: CALIFORNIA: Los Angeles Co.: *Anderson 132* (WTU), *Bacigalupi 4201* (CAS, JEPS, RM, UTC), *Bacigalupi & Alava 6426* (JEPS), *Elmer 3700* (DS, GH, MO, POM, US, WTU), *Ewan 7216* (POM), *Goodman & Hitchcock 1722* (MO, NY, RM), *Pierson 2440* (JEPS, RSA). Ventura Co.: *Hall 6598* (DS, UC, US).

Affinities of ssp. *gabriellensis* and evolutionary relationships of infraspecific taxa within *Hulsea vestita* remain unclear. These taxa are primarily separated by combinations of morphological characters that vary in a quantitative but discontinuous fashion. Intersubspecific hybrids were produced with relative ease and, with the exception of hybrids involving ssp. *pygmaea*, were characterized by normal meiosis and comparatively high pollen fertility. These data suggest that evolution within the complex has not been accompanied by selection from genetic barriers to cross-compatibility nor by major chromosomal reorganization. Distribution of the several subspecies is largely allopatric. Although sympatric with ssp. *vestita* in the Sierra Nevada and with ssp. *parryi* in the San Bernardino Mts., ssp. *pygmaea* is restricted to alpine or subalpine sites while the former taxa are associated with coniferous forest at lower elevations. It is likely, then, that differentiation has primarily been associated with geographical and ecological isolation. Maximum isolation of populations probably was last achieved during the Xerothermic period, some 8500 to 3000 years ago (Heusser, 1960). During this period, the distribution of coniferous forest was probably restricted to only the highest elevations in the mountains of southern California (Axelrod, 1966). Earlier glacial-interglacial cycles also contributed to fluctuations in elevational distribution of coniferous forest. As suggested by Axelrod, such conditions favored population instability and local isolation. I suggest that these conditions also contributed to differentiation within *Hulsea vestita*, as is indicated by the strongly insular patterns of morphological variations within the complex.

ACKNOWLEDGMENTS

I thank Michael Amling for writing the computer program, Janice Beatley for collection of ssp. *inoensis*, and Robert P. Adams for advice concerning the numerical analysis.

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AN INTERSECTIONAL HYBRID IN HEMIZONIA (COMPOSITAE: MADIINAE)

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The tarweed genus *Hemizonia* consists of 25 annual and six perennial species that bloom in late spring, summer, and fall. They occur throughout the Coast Ranges and valleys of California, northern Baja California, and the adjacent offshore islands. Two of the annual species found in the Southern Coast Ranges are *Hemizonia australis* (Keck) Keck (sect. *Centromadia*, $n = 11$) and *H. ramosissima* Benth. (sect. '*Deinandron*' sensu Keck, $n = 12$). [Apparently Keck (1935, 1958, 1959) did not formally establish this section; it will probably be designated as sect. *Hartmannia* (Gray) Gray (1874, 1876; Tanowitz, ined.)]. Distributions of these two species overlap in the low-lying coastal regions of Santa Barbara County where six intersectional hybrids were discovered. This hybrid combination is apparently rare.

Intersectional hybrids have been described in a number of genera such as *Ceanothus* (Nobs, 1963; Hannan, 1974), *Crepis* (Babcock and Stebbins, 1938), *Ribes* (Keep, 1962), *Helianthus* (Heiser et al., 1962), and *Perityle* (Powell, 1970). A number of intersectional hybrid attempts in *Hemizonia* were made by Clausen (1951). All were highly sterile except for a quite fertile one between *H. pungens* (H. & A.) T. & G. (sect. *Centromadia*, $n = 9$) and *H. ramosissima*. *Hemizonia pungens*, although well differentiated from other members of its section, clearly